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A NEW XYSTODESMID MILLIPED GENUS AND THREE NEW SPECIES FROM THE EASTERN BLUE RIDGE MOUNTAINS OF NORTH CAROLINA (POLYDESMIDA)

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Abstract.—The new xystodesmid milliped genus *Prionogonus* is proposed for three new species—*haerens, divaricatus,* and *thrinax*—in the eastern Blue Ridge Mountains and Blue Ridge escarpment of southwestern North Carolina. A row of blunt or sharply pointed spurs along the lateral side of the basal zone of the gonopodal acropodite, not found in any other apheloriine genus, characterizes *Prionogonus,* which is also distinguished by the absence of a distal zone and apical curve from the acropodite and by the presence of a solenomerite. Specific differences include the length of the row of spurs, the overall configuration and apical features of the acropodite, and the position and configuration of the solenomerite. The species are allopatric but occur close together in limited ranges. The distribution of *haerens,* much larger than that of either of the others, covers over half the generic range, which is the smallest in the tribe Apheloriini. *Prionogonus* is a "sigmoid" genus and may share common ancestry with *Sigmoria stibarophalla* Shelley. The species *haerens* and *divaricatus* evolved from a common ancestor, but *thrinax* is more distant.

This contribution concerns a group of "sigmoid" xystodesmid millipeds that inhabits a small area in the southern Blue Ridge Mountains and whose existence has been known for several years. Diagnoses were deferred until taxonomic confusion among the established "sigmoid" genera—*Sigmoria, Sigiria,* and *Falloria*—could be resolved, because I did not want to risk having to synonymize a new genus on the basis of revised concepts of existing genera. I have now demonstrated that *Sigiria* and *Falloria* are synonyms of *Sigmoria,* and broadened the concept of this taxon to encompass a diversity of forms whose gonopods conform to a particular pattern (Shelley 1981a). The gonopods of the xystodesmids discussed herein differ significantly from this pattern, leaving no doubt that they represent a new apheloriine genus.

I defined *Sigmoria* to include forms in which the gonopodal acropodite curves through one or more vertical planes and consists of three major sections labeled "basal zone," "peak," and "distal zone" (Shelley 1981a) (see gonopod terminology section under taxonomic characters). The basal zone and peak are separated by a broad or sharp "anterior bend," and the acropodite usually displays an "apical curve," which is formed by the distal zone. Every species of *Sigmoria* except one possesses a flange on the medial face of the acropodite, either on the proximal portion of the peak or on the proximal portion of the distal zone. Although the tip of the acropodite is variable, there is no solenomerite; the acropodite tapers to a single apical termination, on which the prostatic groove opens. Two species differ from aspects of this pattern. *Sigmoria nantahalae* Hoffman

lacks a medial flange, and the distal zone and apical curve are absent from *S. truncata* Shelley. Both of these species otherwise conform to the generic definition and are easily accommodated by *Sigmoria.* Because the three species described herein have gonopods that differ markedly from the above plan, broadening the concept of *Sigmoria* to include them would destroy the homogeneity the genus now possesses. These new species all lack the distal zone and apical curve, and the acropodites terminate at the distal extremities of the peaks. Thus, the consistent absence of the distal part of the acropodite cannot be interpreted as an individual secondary modification of the basic *Sigmoria* plan, as is possible in the case of *S. truncata,* but instead represents an entirely different gonopodal pattern. Furthermore, these three species all possess a distinct solenomerite. In one species the acropodite ends in three acute projections, with the central one carrying the prostatic groove, and in the others the solenomerite is located beneath the distal extremity of the peak so as to form a separate projection from the ending of the acropodite proper. All three species exhibit one *Sigmoria* trait—a medial flange on the proximal portion of the peak. All three additionally display a distal tooth on the flange, which may be homologous to the tooth of some species of *Sigmoria,* particularly those of the *latior* species group. However, two of the new species also possess a lateral flange on be peak opposite the medial flange, a feature not shared with species of *Sigmoria.* Finally, all three new species possess a row of distinct spurs on the lateral side of the basal zone, a feature unique to "sigmoid" xystodesmids. The tubercles of *S. tuberosa* Shelley are neither homologous nor analogous to the spurs, since they are much smaller and are clustered basally.

Thus, these three new species represent a new "sigmoid" genus—*Prionogonus*—whose name refers to the spurs on the basal zone. Its species are distinguished by the overall configuration and apical characteristics of the acropodite, by the position and configuration of the solenomerite, and by the length of the row of spurs. Either I or an assistant collected most of the material on which this paper is based, and our specimens are deposited in the invertebrate collection of the North Carolina State Museum of Natural History (NCSM). In the ensuing species accounts the collector's name is omitted for samples taken by me alone, and the NCSM invertebrate catalog number is indicated in parentheses after appropriate locality citations. Four samples of the most widely distributed species were discovered in the collection of the Museum of Comparative Zoology (MCZ) and the private holdings of Richard L. Hoffman (RLH). Paratypes of all three species were deposited in the Florida State Collection of Arthropods (FSCA), Gainesville.

Taxonomic Characters

The taxonomic characters of *Prionogonus* are found exclusively on the gonopods. Color pattern is of no taxonomic value because sympatric species of *Sigmoria* also exhibit the red paranota and metatergal stripes seen in *Prionogonus.* The length and configuration of the process of the 4th sternum also differ in each species (longer than the adjacent coxal widths in *haerens,* slightly shorter than the coxae and deeply divided apically in *divaricatus,* and much shorter than the coxae and with four long apical setae in *thrinax*), but it would be very risky to

base identifications on this structure alone. Differences between this process in species of *Prionogonus* and sympatric species of *Sigmoria* are of insufficient magnitude to allow for authentic determinations.

The most important and obvious diagnostic character of the gonopods of *Prionogonus* is the row of spurs on the lateral side of the basal zone. No other xystodesmid genus in the eastern United States possesses such a feature.

At the species level, the taxonomically useful characters are located solely on the acropodites, as differences in the size and configuration of the prefemoral processes are too insigifinicant to be reliable. The greatest utility of the spurs is in distinguishing *divaricatus* from its congeners. In this species the spurs extend around the anterior bend onto the peak and terminate at the base of the lateral flange. The spurs on both *haerens* and *thrinax* are restricted to the basal zone; they are smaller and fewer in number in *thrinax,* but this difference is of little taxonomic use.

The overall configuration of the acropodite is an important taxonomic character. In *thrinax* the anterior bend is broad and poorly defined, and the acropodite forms a smoothly continuous arc of broad diameter. In *haerens* and *divaricatus* the anterior bend is sharp, approximately a right angle, and the configuration of the acropodite resembles an inverted L. The peak of the acropodite is slightly longer in *divaricatus* and hence overhangs the prefemoral process to a greater degree than in *haerens*. Consequently, the relative proportions of the basal zone and peak to the total length of the acropodite also differ in these two species. Each region represents about half of the total acropodite length in *divaricatus,* whereas the basal zone comprises about two-thirds, and the peak one-third, of the length in *haerens*.

Apically on the acropodite, the three-pronged termination, the subspiniform solenomerite directed away from the gonopod along the axis of the acropodite, and the presence of the lateral process are all diagnostic for *thrinax*. In separating *haerens* from *divaricatus,* fusion or segregation, respectively, of the acropodite and the undersurface of the peak are the most important diagnostic features. Of nearly equal taxonomic value, however, is the size of the tooth on the medial flange. In *divaricatus* it is large and extends to the level of the distal extremity of the peak, but in *haerens* it is reduced, vestigial, or absent, and terminates proximal to the end of the peak when present.

Prionogonus, new genus

Type species.—Prionogonus haerens, new species.

Description.—A genus of moderate-size xystodesmids with the following characteristics:

Body composed of head and 20 segments in both sexes; size varying from around 40–45 mm in length and 9.5–11.5 mm in width; W/L ratio similarly varying from about 22.5–25.5%. Body essentially parallel-sided in midbody region, tapering at both ends.

Color in life constant; all forms with red paranota and red connecting stripes along caudal edges of metaterga, with additional red connecting stripe along anterior edge of collum.

Head of normal appearance, smooth, polished. Epicranial suture thin but distinct, terminating in interantennal region, not apically bifid; interantennal isthmus varying from around 1.5–2.0 mm; genae not margined laterally, with shallow central impressions, ends broadly rounded and projecting slightly beyond adjacent cranial margins. Antennae moderately slender, relatively constant in length, becoming progressively more hirsute distally, with 4 conical sensory cones on ultimate article; no other sensory structures apparent. Facial setae reduced; epicranial and interantennal absent, frontal and genal present or absent, clypeal and labral present.

Terga smooth and polished, becoming moderately coriaceous in paranotal regions, especially on anterior half of paranota. Collum broad but variable, ends subequal to or extending slightly beyond those of following tergite. Paranota moderately to strongly depressed but generally continuing slope of dorsum, anteriolateral corners rounded on all segments, caudolateral corners rounded on anteriormost segments, becoming blunt in midbody region and progressively more acute posteriorly. Peritremata flat and indistinct, especially in anterior third of body, not strongly elevated above metazonal surface; ozopores located just caudal to midlength, opening dorsad. Prozonites smaller than metazonites; strictures moderately distinct, slightly costulate.

Caudal segments normal for family.

Sides of metazonites generally smooth, without grooves or impressions. Pregonopodal sterna of males variously modified; that of segment 4 with medial process of variable length, shorter to longer than widths of adjacent coxae, with or without apical setae; sternum of segment 5 with two distinct or medially coalesced processes between 4th legs, usually slightly shorter than widths of adjacent coxae, with variable elevated areas or knobs between 5th legs; sternum of segment 6 with minute processes between 6th legs and with shallow convex recession between 7th legs to accommodate apical regions of acropodites when body segments compressed; 7th legs occasionally set slightly farther apart than 6th. Postgonopodal sterna with bicruciform impressions on first few segments, becoming flattened and plate-like posteriorly with small central impressions, without noticeable lobes along caudal edges between posterior segmental legs. Gonopores on second pair of legs of males short, with round, apical knobs. Coxae with varying distomedial projections beginning on midbody (postgonopodal) legs, usually low, blunt tubercles, occasionally more acute; prefemoral spines relatively long and sharply pointed; tarsal claws hooked or bisinuate. Hypoproct broadly rounded; paraprocts with margins strongly thickened.

Gonopodal aperture elliptical, indented and slightly narrower anteriolaterally, sides flush with or elevated above metazonal surface. Gonopods *in situ* with acropodites projecting ventrad from aperture, bending anteromediad and crossing midline of aperture, curving smoothly over opposite side of aperture and terminating either over aperture or slightly beyond anterior margin, either overlapping each other in midline of aperture or curving in front of and behind each other. Coxae moderate, without apophysis, connected by membrane only, no sternal remnant. Prefemora moderate in size, with small but variable, apically blunt prefemoral processes arising on anteriomedial sides. Acropodites moderately thick and heavy, well sclerotized, curving through mostly a single vertical plane, bent

sharply anteriad (anterior bend) at ⅓ to ½ of total length or curving through continuous arc of broad diameter, terminating distal to anterior bend in peak region; portion between prefemur and anterior bend (basal zone) with row of spurs along lateral margin; spurs variable in length, acuteness, and degree of separation, terminating on basal zone or continuing around anterior bend onto peak; anterior bend either sharp, 90°, and well defined, or broad and poorly defined; portion distal to anterior bend (peak) varying from ⅓ to ½ of total acropodite length, extending to or slightly beyond level of prefemoral process, with flange of variable width and length on medial side, with or without similar flange on lateral side; medial flange with slightly convex margin, usually with small to moderate, subacute tooth at distal corner, tooth either extending to level of distal extremity of peak or terminating short of this point, either directed away from gonopod along axis of acropodite or downward toward coxa and subperpendicular to axis; lateral flange subequal to or slightly longer than medial flange, usually subequal in width to medial flange, margin broadly wavy to nearly straight; lateral terminal process present only when lateral flange absent, moderately long, subacute apically; solenomerite either a bisinuate process fused to or narrowly separated from distal extremity of peak, located beneath and directed laterad, perpendicular to peak, or a long, subspiniform, apically recurved projection directed away from gonopod along axis of acropodite, widely separated from lateral process and tooth of medial flange forming trifurcate termination to acropodite. Prostatic groove arising in pit on medial side of prefemur, crossing to lateral side of acropodite on basal zone just distal to juncture with prefemur, running along stem of acropodite on lateral side and opening terminally on tip of solenomerite.

Cyphopodal aperture short and very broad, encircling 2nd legs, sides elevated above metazonal surface. Cyphopods *in situ* located lateral to 2nd legs, with corner of receptacle and valves visible in aperture, valves directed caudad, oriented dorsoventrally in body. Receptacle variable, moderate to large, located on anterior and lateral sides of valves, cupped over ventral corner of valves in two species, with or without noticeable lobes on anterior and lateral sides, surface rugulose with distinct folds and ridges. Valves moderate in size, either subequal or medial (inner) one slightly larger, surface generally smooth, finely granulate. Operculum minute, located under free (dorsal) end of valves.

Distribution.—Eastern Blue Ridge Mountains and the Blue Ridge escarpment of southwestern North Carolina, ranging from the southern edge of the Black Mountains in McDowell and Buncombe counties to near the Green River on the Henderson-Polk counties line. In the north-south direction the area extends some 26 miles from slightly north of I-40 near the towns of Black Mountain and Old Fort to about four miles north of I-26 and the towns of Flat Rock and Saluda. In the north, the east–west distribution extends from near Swannanoa to Old Fort, a distance of about 13 miles, whereas in the south, the range narrows to a point about four miles north of Saluda.

Species.—Three. One wide-ranging species occupies the northern half of the range; the southern half is inhabited by all three species, the other two having restricted ranges. One or two undiscovered species may exist in inaccessible parts of the southern half of the range, as explained in the distribution section of the paper.

Key to Species of *Prionogonus* (based on adult males)

1. Acropodite with trifurcate termination, solenomerite directed away from gonopod along axis of acropodite; acropodite a broad continuous curve, anterior bend poorly defined; Polk and Henderson counties .... *thrinax,* new species
– Acropodite termination blunt to subacute, with at most two terminal projections; solenomerite located beneath distal extremity of peak, directed perpendicularly and laterad to peak; acropodite bent sharply at ⅓ to ½ length, anterior bend well defined 2
2. Solenomerite fused to undersurface of peak; spurs moderate in size, located entirely on basal zone; McDowell, Buncombe, and Henderson counties ..... *haerens,* new species
– Solenomerite a separate bisinuate process, narrowly segregated from peak; spurs moderate to large in size, extending around anterior bend to base of lateral flange on peak; Rutherford, Henderson, and Polk counties ... . *divaricatus,* new species

Prionogonus haerens, new species
Figs. 1–4

Type-specimens.—Male holotype (NCSM A988) and six male and five female paratypes collected by R. M. Shelley, 12 July 1976, from Buncombe County, NC, 12.6 mi. SE Asheville, along US highway 74, 0.4 mi. W Henderson County line. One male and two female paratypes taken by same collector on same date, 12.4 mi. SE Asheville, along US highway 74, 1.0 mi. W Henderson County line. Male and female paratypes deposited in FSCA and RLH.

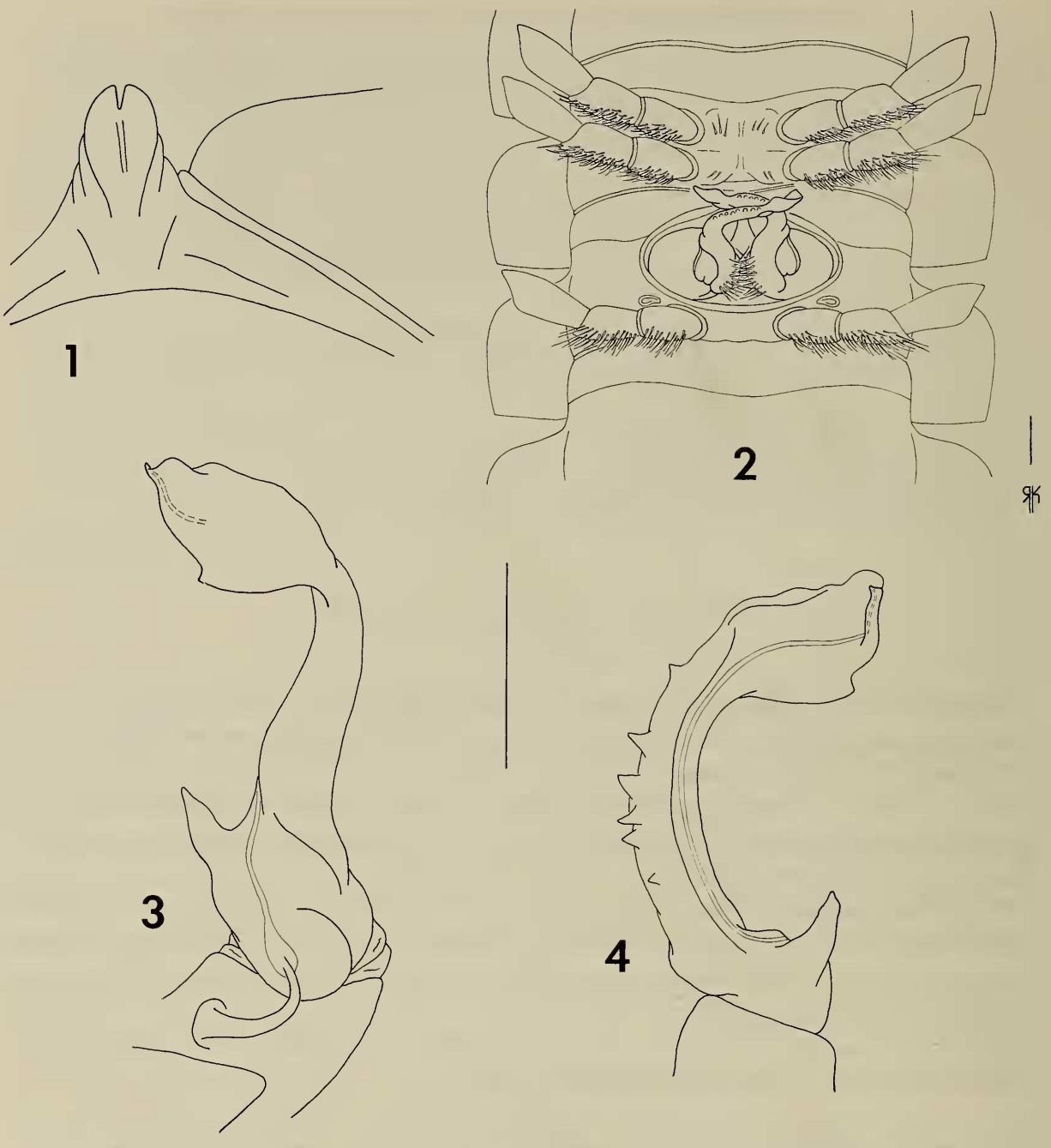
Diagnosis.—Characterized by fusion of solenomerite to undersurface of distal extremity of peak; tooth of medial flange absent, vestigial, or moderate in size, not projecting to level of distal extremity of peak; spurs moderate in size, occurring only on basal zone.

Holotype.—Length 41.9 mm, maximum width 9.6 mm, W/L ratio 22.9%, depth/width ratio 58.3%. Segmental widths as follows:

collum	6.4 mm	12th–14th	9.4
2nd	8.3	15th	9.0
3rd	9.0	16th	8.6
4th	9.4	17th	7.5
5th–11th	9.6	18th	5.7

Color in life: paranota red; metaterga black with wide, red, transverse stripes along caudal edges connecting paranotal spots; collum with red stripes along both anterior and caudal margins.

Head capsule smooth, polished, width across genal apices 5.5 mm; interantennal isthmus 1.4 mm, smooth; epicranial suture thin but distinct, terminating in slight impression in interantennal region, not bifid. Antennae moderately long and slender, reaching back to middle of paranota of third segment, becoming progressively more hirsute distally, with four terminal sensory cones, no other sen-



Figs. 1–4. *Prionogonus haerens:* 1, Process of 4th sternum of holotype, caudal view (leg setation omitted in all sternal drawings); 2, Gonopods *in situ,* ventral view of holotype; 3, Left gonopod of holotype, medial view (setation omitted in all dissected gonopod drawings); 4, The same, lateral view. Scale line for Fig. 2 = 1.00 mm; line for other Figs. = 0.75 mm for 1, 1.00 mm for 3–4.

sory structures evident, relative lengths of antennomeres 2 > 3 > 4 = 5 = 6 > 1 > 7, 1 subglobose, 2–6 clavate, 7 short and truncate. Genae not margined laterally, with distinct medial impressions, ends broadly rounded and projecting slightly beyond adjacent cranial margins. Facial setae as follows: epicranial, interantennal, frontal, and genal absent, clypeal about 10–10, labral about 20–20.

Terga smooth, polished, becoming moderately coriaceous on paranota. Collum broad, ends extending slightly beyond those of following tergite, caudal edge relatively straight. Paranota moderately depressed, angled ventrad and continuing

slope of dorsum; anterior corners rounded; caudolateral corners rounded only on first three tergites, blunt on segments 4–15, becoming acute and pointed on remaining segments. Peritremata shallow, indistinct on first eight segments; only slightly elevated above metazonal surface thereafter. Ozopores located caudal to midlength of peritremata, opening dorsad.

Sides of metazonites smooth, generally without grooves or impressions; strictures sharp and distinct. Gonopores short and knob-like. Sternum of segment 4 (Fig. 1) with relatively long, apically divided process, slightly longer than widths of adjacent coxae; sternum of segment 5 with two elevated areas between 5th legs and distinct processes between 4th legs, coalesced medially, only slightly shorter than widths of adjacent coxae; sternum of segment 6 with two faint knobs between anterior legs and shallow, convex, recession between posterior legs to accommodate gonopodal acropodites. Postgonopodal sterna with bicruciform impressions on segments 8–10, becoming flat and plate-like posteriorly. Coxal tubercles beginning on caudal legs of segment 9, becoming sharply pointed on segment 10 and continuing to segment 17; prefemoral spines beginning on caudal legs of segment 5 and continuing to ultimate leg pair, becoming progressively longer and sharper caudally; tarsal claws hooked, not bisinuate. Hypoproct rounded; paraprocts with margins strongly thickened.

Gonopodal aperture elliptical, 3.4 mm wide and 1.5 mm long at midpoint, indented on anteriolateral margins, sides raised above metazonal surface. Gonopods *in situ* (Fig. 2) with acropodites crossing in midline of aperture, extending foward slightly beyond anterior margin of aperture. Gonopod structure as follows (Figs. 3–4): coxae moderate in size. Prefemur moderate, with moderately long, apically blunt prefemoral process arising on anterior side, directed toward point beyond tip of acropodite. Acropodite moderately thick and heavy, configuration that of inverted L, tip not extending beyond level of prefemoral process; basal zone long, about ⅔ of acropodite length, with row of six blunt to sharply pointed spurs on lateral side; spurs irregularly spaced, beginning near base of basal zone and terminating near anterior bend; anterior bend sharp and well defined, approximately a right angle; peak short, about ⅓ of acropodite length; medial flange shorter than peak, margin continuous, with blunt tooth on distal corner, tooth directed outward away from gonopod, continuous with axis of acropodite, not projecting to level of distal extremity of peak; lateral flange subequal in width, but slightly longer than, medial flange, extending entire length of peak, margin wavy; solenomerite a short bisinuate process fused to undersurface of distal extremity of peak, much shorter than width of distal extremites of peak and flanges, directed laterad, perpendicular to axis of acropodite. Prostatic groove crossing to lateral side on proximal portion of basal zone, running along lateral side of acropodite stem and under surface of peak to opening at distal corner of solenomerite.

Male paratypes.—The male paratypes agree with the holotype in somatic features. On the gonopods the tooth on the medial flange is missing in several specimens, and the prefemoral process is more globose basally in some. Otherwise, the gonopods are very similar, and all possess six spurs on the basal zone. The distance between spurs and their relative lengths vary slightly.

Female paratype.—Length 44.3 mm, maximum width 10.4 mm, W/L ratio 23.5%, depth/width ratio 69.2%. Agreeing closely with holotype in somatic details except

paranota more strongly depressed, giving appearance of more highly arched dorsum, and caudolateral corners of paranota more rounded.

Cyphopodal aperture extending around 2nd legs, sides raised above metazonal surface. Cyphopods *in situ* with corner of receptacle and valves visible in aperture, valves directed caudad, oriented dorsoventrally in body. Receptacle moderately large, cupped around ventral end of valves, surface rugulose. Valves moderate in size and subequal, surface finely granulate. Operculum minute, situated under dorsal corner of valves.

Variation.—The most variable aspects of the *haerens* gonopod are the configurations of the medial flange and prefemoral process, and the number, position, and shape of the spurs. In a few males the peak is also longer than that of the holotype and overhangs and extends slightly beyond the level of the prefemoral process. Variation in the configuration of the medial flange is as described under male paratypes; the tooth is vestigial or absent from about ⅓ of the individuals collected, and in a few specimens it is longer and more pronounced than in the holotype. The prefemoral process is elongate in males collected near Fairview, Buncombe County, but the configuration in the holotype is about average for the species. The spurs range in number from six to eight and may be more or less evenly spaced along the basal zone, or clustered near the distal extremity. They range from sharply pointed and subspiniform to low and blunt; usually the basal and distalmost spurs are smaller than the others. The configuration of the solenomerite is mostly as described for the holotype, although it is considerably narrower in a few males.

Distribution.—A subrectangular area ranging from the vicinity of Old Fort, McDowell County, and Black Mountain (town), Buncombe County, in the north, to just south of US highway 74 in Hickorynut Gorge, Henderson County, in the south (Fig. 14). North Carolina state highway 9, connecting Black Mountain and Bat Cave, bisects the range. The species is clustered in the northern and southern extremes of the range. It is relatively common near Swannanoa, Black Mountain, and Old Fort, in the north, and in the Hickorynut Gorge area between Fairview and Bat Cave, in the south. An apparent distributional hiatus occurs in east-central Buncombe County. Specimens were examined as follows:

NORTH CAROLINA: *McDowell Co.,* 4.4 mi. N Old Fort, along co. rd. 1409, 0.2 mi. W jct. co. rd. 1408, 2M, 10 September 1977 (NCSM A1724); and 4.0 mi. N Old Fort, along US Forest Serv. Rd. in Pisgah Nat. For., M, 10 September 1977 (NCSM A1723). *Buncombe Co.,* 3.2 mi. NW Black Mountain, along co. rd. 2476, 1.7 mi. N jct. co. rd. 2474, M, 5 September 1977 (NCSM A1702); Black Mountain, M, September 1901, collector unknown (RLH) and 5M, 4F, date and collector unknown (MCZ); 2 mi. N Swannanoa, along co. rd. 2427, 1.0 mi. N jct. co. rd. 2429, M, 5 September 1977 (NCSM A1703); 5.2 mi. NE Asheville, along co. rd. 2424, 1.0 mi. N jct. co. rd. 2419, M, 5 September 1977 (NCSM A1704); 8 mi. SE Fairview, W side Hickorynut Gap, 2M, 2 August 1973, R. L. Hoffman and L. S. Knight (RLH); 12.2 mi. SE Asheville, along co. rd. 2806, 0.1 mi. W jct. co. rd. 2809, M, 12 July 1976 (NCSM A989); and 12.4–12.6 mi. SE Asheville, along US hwy. 74, 0.4–1.0 mi. W Henderson co. line 10M, 7F, 12 July 1976 and 9 September 1977 (NCSM A979, A988, and A1721) TYPE LOCALITY. *Henderson Co.,* 2 mi. NE Gerton, along co. rd. 1606, 0.2 mi. W jct. co. rd. 1605, M, 13 September 1977 (NCSM A1739); 3.7 mi. NW Bat Cave, along US hwy. 74,

0.8 mi. E jct. co. rd. 1598, 2M, 3F, 12 July 1976 (NCSM A1005); 1 mi. S Bat Cave, along US hwy. 64, Hickorynut Gap, M, 2F, 13 July 1962, R. L.Hoffman (RLH); 1 mi. SW Bat Cave, along US hwy. 64, jct. co. rd. 1514, 2M, 4F, 12 July 1976 (NCSM A1000); 9.6 mi. NE Hendersonville, along co. rd. 1569, 0.3 mi. W jct. co. rd. 1595, M, 2F, 12 July 1976 (NCSM A999); and 6 mi. E Fletcher, along co. rd. 1569, 1.0 mi. W jct. co. rd. 1594, M, 2F, 13 September 1977 (NCSM A1737).

Remarks.—*Prionogonus haerens* occupies a much larger area than either of its congeners. It is the only species in the northern half of the generic range, and it extends into the southern half to south of Hickorynut Gorge. The other two species occur only in the southern and eastern fringes of the range, and they are the only "sigmoid" species in this area. The area inhabited by *haerens* abuts that of the next species and traverses parts of the ranges of three other sympatric "sigmoid" xystodesmids: *Sigmoria rubromarginata* (Bollman) in McDowell and eastern Buncombe counties, the area occupied by intergrades; *S. stibarophalla* Shelley, along NC highway 9 in eastern Buncombe County; and *S. stenogon* Chamberlin, in northern Henderson County. Thus, species determinations from within the range of *haerens* must be done carefully on mature males only; *haerens, rubromarginata,* and *stibarophalla* all have red paranota and stripes and can easily be confused. *Sigmoria stenogon,* which has purple paranota and stripes in most of its range (Shelley 1981a), takes on a reddish tint in northern Henderson County, and it too can be confused with *haerens*. Although *haerens* occurs sympatrically with these three species, they are not microsympatric, and *haerens* has never been collected along with another "sigmoid" xystodesmid at a single site. Thus, the competitive exclusion principle, which holds for species of *Sigmoria* (Shelley 1981a), also applies for species of *Prionogonus*.

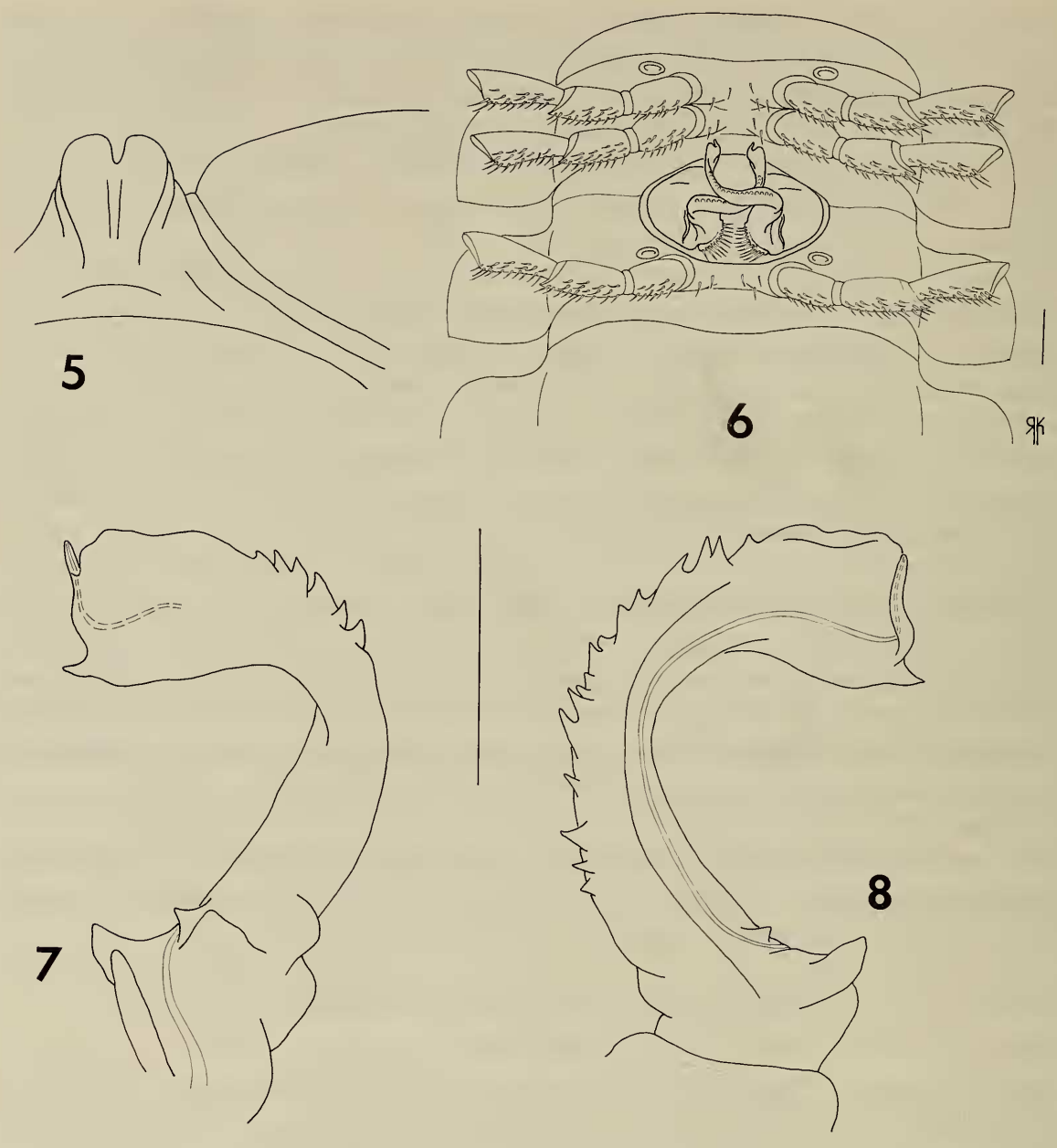
Prionogonus divaricatus, new species
Figs. 5–8

Type-specimens.—Male holotype (NCSM A2035) and four male and three female paratypes collected by R. M. Shelley and W. B. Jones, 7 June 1978, from Polk County, NC, 4.8 mi. NW Mill Spring, along county road 1138, 0.3 mi. W junction of country road 1156. Male and female paratypes deposited in FSCA.

Diagnosis.—Characterized by narrow separation of solenomerite from distal extremity of peak; tooth of medial flange generally large, projecting distad to about distal extremity of peak; spurs large and numerous, extending around anterior bend to base of lateral flange on peak.

Holotype.—Length 46.2 mm, maximum width 11.7 mm, W/L ratio 25.3%, depth/width ratio 59.0%. Segmental widths as follows:

collum	8.1 mm	10th–14th	11.4
2nd	9.1	15th	11.1
3rd	10.1	16th	10.4
4th	10.9	17th	8.9
5th	11.2	18th	6.7
6th–9th	11.7		



Figs. 5–8. *Prionogonus divaricatus:* 5, Process of 4th sternum of holotype, caudal view; 6, Gonopods *in situ,* ventral view of paratype; 7, Left gonopod of holotype, medial view; 8, The same, lateral view. Scale line for Fig. 6 = 1.00 mm; line for other Figs. = 1.00 mm for each.

Color in life: paranota red; metaterga black with wide, red, transverse stripes along caudal edges connecting paranotal spots; collum with red stripes along both anterior and caudal edges.

Somatic features similar to those of *haerens,* with following exceptions:

Width across genal apices 5.4 mm, interantennal isthmus 1.9 mm. Antennae reaching back to caudal edge of third paranota, relative lengths of antennomeres $2 > 3 > 4 > 5 = 6 > 1 > 7$. Facial setae as follows: epicranial and interantennal absent, frontal 1–1, genal 1–1, clypeal about 8–8, labral about 13–13, merging with clypeal series and continuing for short distance along genal margins, 4 setae on each side.

Collum broad, extending well beyond margins of following tergite. Paranota strongly depressed, continuing slope of dorsum and angling sharply ventrad, cau-

dolateral corners rounded through segment 5, blunt on segments 6–14, becoming progressively more acute posteriorly.

Process of 4th sternum (Fig. 5) shorter than widths of adjacent coxae and deeply divided apically; knobs and elevated areas on 5th sternum similar to those of *haerens,* knobs betwen 4th legs more distinctly separated; 6th sternum moderately recessed between 7th legs to accommodate ends of acropodites, 7th legs set slightly farther apart than 6th. Postgonopodal sterna bicruciately impressed on segments 8–9, becoming plate-like with shallow central impressions posteriorly. Tarsal claws bisinuately curved.

Gonopodal aperture elliptical, 4.2 mm wide and 2.3 mm long at midpoint, indented on anteriolateral margin, sides elevated above metazonal surface. Gonopods *in situ* (Fig. 6, of paratype) with acropodites crossing at midlengths, curving over opposite sides of aperture and anterior margin to between caudal legs of segment 6. Gonopod structure as follows (Figs. 7–8): prefemoral process short and blunt, directed toward tip of acropodite. Acropodite moderately thick and heavy, configuration that of inverted L, peak overhanging and extending slightly beyond level of prefemoral process; basal zone proportionately shorter than that of *haerens,* about ½ of acropodite length, with spur basally on medial side at juncture with prefemur and row of 10 or so sharply pointed spurs on lateral margin; spurs irregular in length and irregularly spaced, continuing around anterior bend to base of lateral flange on peak, 16 spurs total; anterior bend sharp and well defined, approximately 90°; peak long, about ½ of acropodite length; medial flange arising distal to anterior bend, terminating at distal extremity of peak, margin smoothly continuous, with sharply pointed tooth on distal corner, tooth directed outward away from gonopod, continuous with axis of acropodite, projecting distad to level of distal extremity of peak; lateral flange subequal in width to medial flange, arising near midlength of peak, terminating at distal extremity, margin slightly but smoothly indented; solenomerite a long, blunt, bisinuate process, length about ¾ of width of distal extremity of peak, detached and narrowly separated from peak. Prostatic groove crossing to lateral side on proximal portion of basal zone, running along lateral side of acropodite stem and undersuface of peak to opening at tip of solenomerite.

Male paratypes.—The male paratypes agree with the holotype in all particulars.

Female paratype.—Length 44.9 mm, maximum width 11.1 mm, W/L ratio 24.7%, depth/width ratio 66.7%. Agreeing essentially with males in somatic details, except paranota more strongly depressed, creating appearance of more highly arched body.

Cyphopods *in situ* with corner of receptacle and valves visible in aperture, valves directed caudad, oriented dorsoventrally in body. Receptacle large, cupped over ventral end of valves, surface rugulose. Valves moderate and unequal, inner one slightly larger, surface finely granulate.

Variation.—The gonopods of *divaricatus* are quite uniform. Males from Rutherford County display a bifurcate prefemoral process, and the basal tooth on the medial side of the basal zone is absent from all males except those in the type series. In all specimens the spurs extend beyond the anterior bend onto the peak of the acropodite. The number of spurs varies from about 8 to 14, and they are located mostly distal to midlength of the basal zone. The arch of the acropodite is constant, overhanging and extending slightly beyond the level of the prefemoral

process in all males, and the basal zone and peak are roughly equivalent in length, each comprising approximately ½ of the total length of the acropodite.

Distribution.—A small area centering on the contiguous corners of Henderson, Polk, and Rutherford counties, ranging to the eastern edge of the Blue Ridge escarpment in Polk County. Specimens were examined as follows:

NORTH CAROLINA: *Rutherford Co.,* Lake Lure (town), Bottomless Pool area, 4F, 13 July 1976 (NCSM A1011) and 3M, 5F, 9 September 1978, W. B. Jones (NCSM A2427). *Henderson Co.,* 1.6 mi. SE Edneyville (6.1 mi. NE Hendersonville), along co. rd. 1719, 1.8 mi. NE jct. co. rd. 1720, M 5F, 8 June 1978, R. M. Shelley and W. B. Jones (NCSM A2043). *Polk Co.,* 7.6 mi. NW Mill Spring, along co. rd. 1163, 1.4 mi. W jct. co. rd. 1161, M, F, 14 September 1977 (NCSM A1743); 7.2 mi. NW Mill Spring, along co. rd. 1162, 0.8 mi. W jct. co. rd. 1161, M, 2F, 7 June 1978, R. M. Shelley and W. B. Jones (NCSM A2034); and 4.8 mi. NW Mill Spring, along co. rd. 1138, 0.3 mi. W jct. co. rd. 1156, 5M, 3F, 7 June 1978, R. M. Shelley and W. B. Jones (NCSM A2035) TYPE LOCALITY.

Remarks.—The gonopods of *divaricatus* are similar in appearance to those of *haerens,* and one might justifiably wonder if the two are not subspecifically related. However, I think that the differences, coupled with their contiguous ranges in northeastern Henderson County, indicate reproductive isolation. Among the gonopodal differences are the following: the length of the acropodal arc, which is longer in *divaricatus* and overhangs the prefemoral process to a greater degree; fusion of the solenomerite to the undersurface of the peak in *haerens,* whereas they are separate in *divaricatus*; the more pronounced tooth on the medial flange of *divaricatus*; the greater number of spurs in *divaricatus* and their extension around the anterior bend onto the peak; and the longer prefemoral process of *haerens*. Somatically, the paranota of *divaricatus* are more strongly depressed in males, and the process of the 4th sternum is also shorter than the widths of the adjacent coxae, whereas it is longer than the coxae in *haerens*. These are considerable differences between species whose ranges are contiguous, and there is no possibility for clinal gradation between them. This geographic pattern is markedly different from patterns displayed by other "sigmoid" species that are divided into subspecies, species such as *S. latior* (Brolemann), *S. rubromarginata* (Bollman), and *S. nigrimontis* (Chamberlin) (Shelley 1981a). The evidence therefore supports my belief that *haerens* and *divaricatus* are reproductively isolated, thus valid species.

Prionogonus thrinax, new species
Figs. 9–12

Type-specimens.—Male holotype (NCSM A2041) and two male and one female paratypes collected by R. M. Shelley and W. B. Jones, 8 June 1978, from Henderson County, NC, 3.1 mi. NE Flat Rock, along county road 1802, 0.7 mi. E junction of county road 1801. One male and one female paratypes collected by W. B. Jones, 9 September 1978, from Henderson County, along county road 1802, 2 mi. E junction of county road 1801. Male paratype deposited in FSCA.

Diagnosis.—Distinguished from congeners by trifurcate termination of acropodite, comprised of tooth of medial flange, subspiniform solenomerite, and a lateral process, tooth directed subperpendicularly to axis of acropodite, others

directed along axis and away from gonopod; also characterized by smoothly continuous arc of acropodite with broad, poorly defined anterior bend; reduction in size and number of spurs on basal zone, and by reduction of lateral flange.

Holotype.—Length 40.8 mm, maximum width 9.7 mm, W/L ratio 23.8%, depth/width ratio 61.9%. Segmental widths as follows:

collum	6.6 mm	15th	9.3
2nd	8.0	16th	8.9
3rd	9.0	17th	8.0
4th–5th	9.4	18th	6.0
6th–14th	9.7		

Color in life: paranota red; metaterga black with wide, red, transverse stripes along caudal edges connecting paranotal spots; collum with red stripes along both anterior and caudal edges.

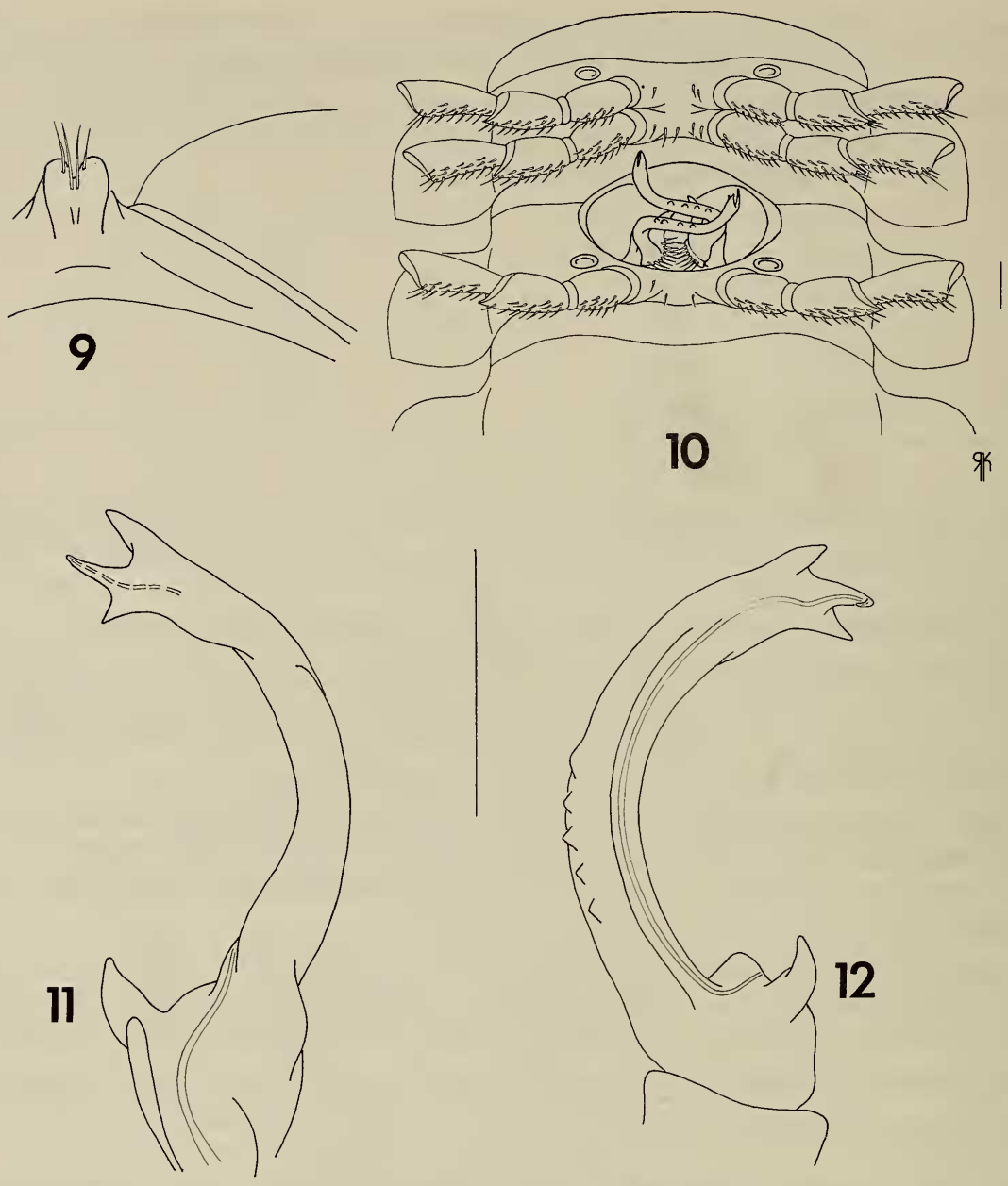
Somatic features similar to those of *haerens,* with following exceptions:

Width across genal apices 4.6 mm, interantennal isthmus 1.5 mm. Antennae reaching back to middle of 3rd paranota, relative lengths of antennomeres $2 > 3 > 4 = 5 > 6 > 1 > 7$. Facial setae as follows: epicranial, interantennal and frontal absent, genal 1–1, clypeal about 12–12, labral about 15–15.

Collum broad, extending slightly beyond ends of following tergite. Paranota moderately depressed, continuing slope of dorsum, caudolateral corners rounded through segment 6, blunt on segments 7–14, becoming progressively more acute posteriorly.

Process of 4th sternum (Fig. 9) small, much shorter than widths of adjacent coxae, with four long apical setae; knobs and elevated areas of 5th sternum distinct, similar to condition in *haerens*; sternum of segment 6 moderately recessed between 7th legs to accommodate ends of acropodite. Postgonopodal sterna with bicruciform impressions on segments 8–10, becoming flat and plate-like posteriorly with shallow central impressions. Tarsal claws bisinuately curved.

Gonopodal aperture elliptical, 3.4 mm wide and 1.8 mm long at midpoint, indented on anteriolateral margin, sides flush with metazonal surface. Gonopods *in situ* (Fig. 10, of paratypes) with acropodites lying generally over opposite side of aperture, not really crossing each other and extending only short distance beyond anterior edge of aperture. Gonopod structure as follows (Figs. 11–12): prefemoral process short, subtriangular, directed toward tip of acropodite. Acropodite relatively thin but sturdy, well sclerotized, configuration a smoothly continuous arc with broad diameter, not sharply divided into zones, extending slightly beyond and overhanging prefemoral process, terminating in three widely separated acute projections—tooth of medial flange, solenomerite, and lateral process; basal zone of indeterminate length, with only 4 to 5 spurs on lateral margin; spurs greatly reduced to size of small tubercles, barely detectable in lateral view, relatively close together, located entirely on basal zone; anterior bend broad, poorly defined, location indeterminate; peak of indeterminate length, terminating in long, sharply pointed solenomerite and shorter, blunter, lateral process, widely separated from solenomerite; medial flange arising distad on acropodite (peak zone?), expanding slightly proximad, with relatively long, acute



Figs. 9–12. *Prionogonus thrinax:* 9, Process of 4th sternum of holotype, caudal view; 10, Gonopods *in situ*, ventral view of paratype; 11, Telopodite of left gonopod of holotype, medial view; 12, The same, lateral view. Scale line for Fig. 10 = 1.00 mm; line for other Figs. = 1.00 mm for 11–12, 1.18 mm for 9.

tooth on distal corner, tooth directed downward toward coxa, subperpendicular to axis of acropodite; lateral flange absent, perhaps represented by lateral terminal process of acropodite, peak not noticeably expanded on lateral side; solenomerite long and sharply pointed, subspiniform, recurved slightly on underside, directed along main axis of acropodite; lateral terminal process shorter than solenomerite but longer than tooth of medial flange, relatively wide basally, subacute apically, widely separated from solenomerite. Prostatic groove crossing to lateral side on proximal portion of basal zone, running along lateral side of acropodite stem and undersurface of peak to opening at tip of solenomerite.

Male paratypes.—The male paratypes agree with the holotype in all particulars.

Female paratype.—Length 44.6 mm, maximum width 10.2 mm, W/L ratio 22.9%,

depth/width ratio 69.6%. Agreeing with holotype in most somatic features except collum not extending beyond ends of following tergite, and paranota more strongly depressed, creating appearance of more highly arched body.

Cyphopods with corner of receptacle and valves visible in aperture, valves directed caudad, oriented dorsoventrally in body. Receptacle smaller than those of congeners, with two lobes, one anterior and other lateral to valves, not cupped over ventral end of valves, surface rugulose. Valves moderate in size and subequal, surface finely granulate.

Variation.—The spurs on the lateral side of the basal zone are much larger and more pronounced in other males of *thrinax*. One male from Henderson County has a slight lateral expansion on the peak, indicative of a reduced lateral flange, but all other specimens lack any indication of this lamella. The tooth on the medial flange in the male from Polk County is greatly reduced and bifurcate apically, and this individual also has a much longer prefemoral process.

Distribution.—Known only from a small area in eastern Henderson and western Polk counties near the Hungry River, a tributary of the Green River. Specimens were examined as follows:

NORTH CAROLINA: *Henderson Co.,* 6.6 mi. ENE Hendersonville, along co. rd. 1734, 1 mi. SW jct. co. rd. 1525, M, F, 8 June 1978, R. M. Shelley and W. B. Jones (NCSM A2042); 3.1 mi. NE Flat Rock, along co. rd. 1802 0.7 mi. E jct. co. rd. 1801, 3M, F, 8 June 1978, R. M. Shelley and W. B. Jones (NCSM A2041) TYPE LOCALITY; and 4.5 mi. NE Flat Rock, along co. rd. 1802, 1.2 mi. W Polk co. line, M, F, 9 September 1978, W. B. Jones (NCSM A2432). *Polk Co.,* 4.0 mi. NNE Saluda, along co. rd. 1154, 1.2 mi. E Henderson co. line, M, F, 9 September 1978, W. B. Jones (NCSM A2431).

Remarks.—The gonopods of *thrinax* bear a remarkable resemblance to those of *Furcillaria aequalis* Shelley, which occurs in piedmont South Carolina (see Shelley 1981b, Figs. 3–4). If the medial flange of *thrinax* were displaced proximad, the two gonopods would be very close indeed. The lateral terminal process of *thrinax* is therefore analogous to the tibial process of *F. aequalis,* both being terminal and subparallel to the solenomerite, but I do not consider the projections homologous. Thus, I did not name the process in *thrinax,* so as not to imply homology. Moreover, the lateral terminal projection is not a generic feature of *Prionogonus,* as it is of *Furcillaria* and *Dynoria,* but rather a specific trait only of *thrinax*. I do not believe that this resemblance of *thrinax* and *F. aequalis* reflects generic affinity between *Prionogonus* and *Furcillaria*; the phenotypic similarity at the specific level seems to be a convergence. It is noteworthy that such different evolutionary branches as the *Sigmoria-Prionogonus-Hubroria* and *Furcillaria-Dynoria* lines can independently produce species with such similar gonopods.

Ecology

Prionogonus is a typical montane "sigmoid" xystodesmid genus, and its species therefore inhabit the same rhododendron cove and river-bottom environments as most species of *Sigmoria*. This habitat was described in detail by Shelley (1981a). The millipeds are found under thin layers of leaves of hardwood species associated with rhododendron, particularly dogwood and red maple, on relatively hard substrates near water sources. *Prionogonus divaricatus,* which occurs east of its

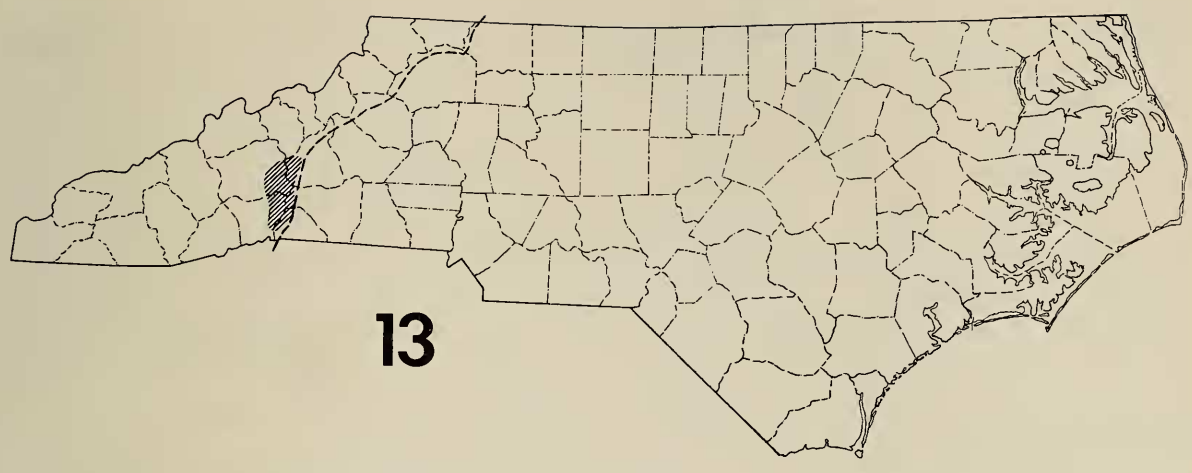
congeners on the Blue Ridge escarpment, begins to penetrate Piedmont-type environments at lower elevations. Rhododendron was scarce at a few sites where it was taken, and the type locality in Polk County, which is near the base of the escarpment, had very little rhododendron and seemed to exhibit more piedmont than montane characteristics. However, *divaricatus* does not extend east onto the Piedmont Plateau proper and cannot be classified as either a truly Piedmont species or as a transprovincial one. It is really a montane xystodesmid that can tolerate more open and drier conditions than most cove dwellers, and can therefore survive in marginal environments combining mountain and piedmont features such as occur on the escarpment. The species was not found east of the type locality, and I suspect that this site is near its eastern range limit.

The type locality of *haerens* was also somewhat atypical in lacking a permanent water source. This locality is on the western side of the Tennessee Valley divide that marks the boundary between Buncombe and Henderson counties, in a headwater drainage area of the French Broad River. No flowing water was present, however, and the millipeds were found just off US highway 74 under leaves in woodland. Occurrence of the normally cove-inhabiting *haerens* at this locality can probably be attributed to the site's being cool, damp, and sheltered, and possessing all the features normally associated with rhododendron coves except a water source.

Distribution

The range of *Prionogonus* (Figs. 13–14) is the smallest of any known apheloriine genus, being approximately 26 miles long and a maximum of only 13 miles wide. Only *Lyrranea* in central Georgia (Hoffman 1963) has a distribution nearly this small, but this genus is monotypic. *Prionogonus* thus has the smallest range of any polytypic milliped genus. The distribution of *Prionogonus* is also broader in the northern half, inhabited by *haerens* alone, than in the southern half, which is occupied by all three species. In the north *haerens* occurs from near Swannanoa to Old Fort, a distance of about 13 miles, but the known area of *thrinax,* the most southerly species, is less than 5 miles wide. Thus, the distribution of *Prionogonus* is wider north of Hickorynut Gorge and US highway 74, and tapers rapidly to the nearly point distribution of *thrinax* in the south, some 4 miles north of Saluda near the Green River. This area does not correlate with any physiographic features, and it straddles the eastern continental divide. *Prionogonus haerens* occurs on both sides of the divide—in the French Broad River basin to the west, and in the Catawba and Broad River drainages to the east. However, *divaricatus* and *thrinax* are limited to the Broad and Green River basins, respectively, both of which drain into the Atlantic Ocean. Although *Prionogonus* is a truly montane genus, *divaricatus,* as mentioned in the ecology section, has spread eastward to the base of the Blue Ridge escarpment and the western edge of the Piedmont Plateau Province.

Hickorynut Gorge is the center of species diversity and abundance in *Prionogonus*. The type-species occurs in the central part of the Gorge around Gerton and Bat Cave in Henderson County, and is also common on the western side of the Gorge in Buncombe County. *Prionogonus divaricatus* occurs on the eastern side of the Gorge around Lake Lure, Rutherford County. However, neither species



Figs. 13–14. 13, Range of *Prionogonus* in North Carolina; 14, Distribution of species of *Prionogonus* in western North Carolina. Dashed line is approximate boundary of southern Blue Ridge Province (Blue Ridge escarpment). Dots, *haerens*; triangles, *divaricatus*; squares, *thrinax*. Each symbol marks a single collecting locality except the southeasternmost one of *haerens*, which represents several samples in the vicinity of Bat Cave.

(nor any other "sigmoid" species) was encountered between Bat Cave and Lake Lure. I investigated the section around Chimney Rock, Rutherford County, several times without finding a single apheloriine milliped, male or female. This area has suitable habitat, and I have no explanation for the apparent absence of the dominant southern Appalachian milliped group from this section of the Gorge.

North Carolina highway 9 bisects the northern half of the generic range in Buncombe County, where *haerens* occurs, and a number of county roads provide access from this route and US highway 74 into the surrounding mountain area. However, the only major highway south of Hickorynut Gorge is US 64, which passes through a corner of the range near Bat Cave. County roads are also limited in the part of the range inhabited by *divaricatus* and *thrinax*, and only one crosses the eastern border of Henderson County between US 74 in Hickorynut Gorge and I-26. *Prionogonus thrinax* was discovered in creek bottoms along this road, but most of the area north of it in eastern Henderson and western Polk and

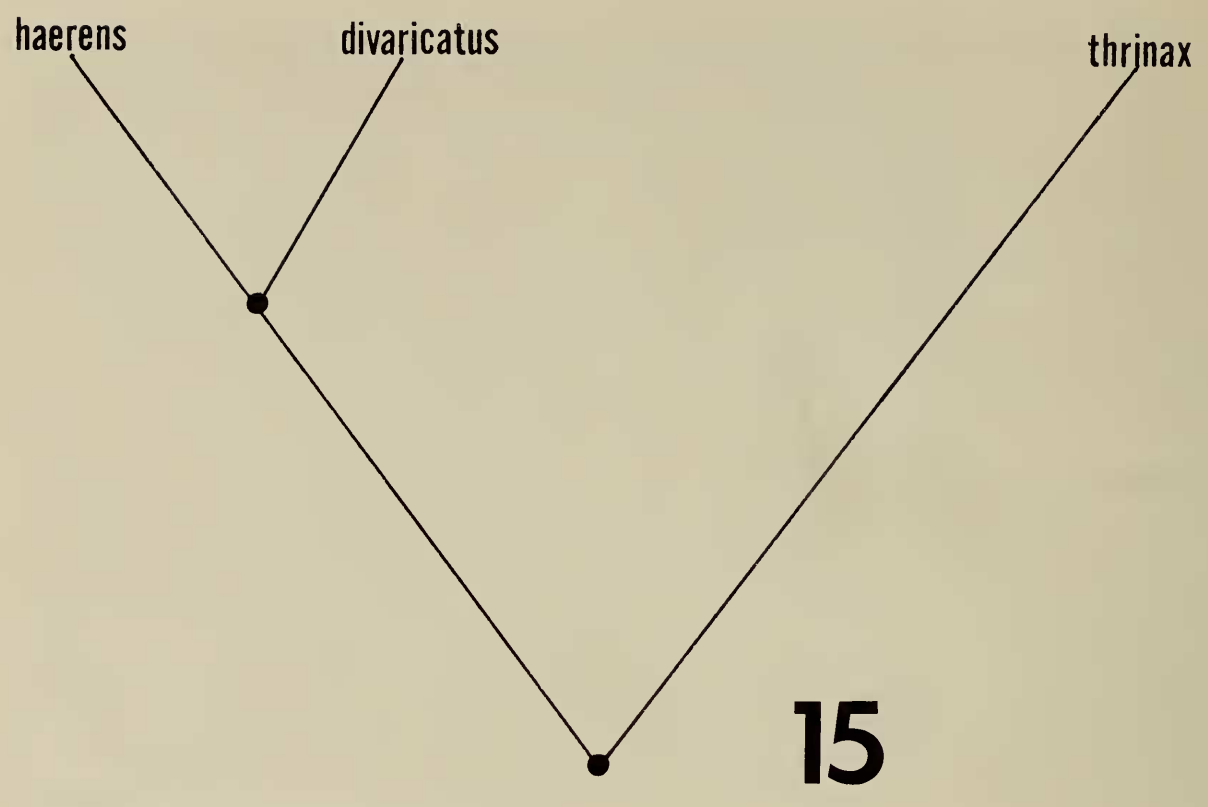


Fig. 15. Relationships in *Prionogonus*.

Rutherford counties was inaccessible and could not be sampled. Since two known species of restricted distribution have evolved in this part of the generic range, it seems possible that others might occur here, especially in the border mountains of Polk-Henderson counties.

Relationships

Generic.— *Prionogonus* is a "sigmoid" xystodesmid milliped genus and is most closely related to *Sigmoria*. Exactly how the two relate is unknown, but the restricted distribution of *Prionogonus* could mean that it is either a recent derivation from "sigmoid" stock, or a remnant of an early fauna that is in a period of decline. The gonopods of *haerens* and *divaricatus* bear some similarity to those of *S. stibarophalla,* which is sympatric with the former, in that the solenomerite is obscured in medial view by the medial flange in all three species. Thus, it can only be examined in lateral perspective. The two species of *Prionogonus* lack a distal zone and apical curve, and the solenomerite is either fused to, or narrowly separated from, the undersurface of the peak. *Sigmoria stibarophalla* has an apical curve and distal zone, but the former is so narrow, and the latter so short, that both are hidden in medial view by the enlarged flange. The more distal crossing from medial to lateral sides of the prostatic groove in *S. stibarophalla,* coupled with the presence of the apical curve and distal zone and the absence of the spurs, are the principle reasons why it is not congeneric with *haerens* and *divaricatus* and instead belongs in *Sigmoria*. The simlarities in the gonopods of *haerens, divaricatus,* and *S. stibarophalla* can best be visualized by comparing figures 4 and 8 in this paper with figure 26 in Shelley (1981a). Perhaps *Prionogonus* shares a common ancestry with *S. stibarophalla*.

The position of the solenomerite beneath the peak, and the absence of a distal zone and apical curve, also suggest the condition in *Cheiropus* and *Stelgipus* in southern Georgia and Florida. I do not mean to suggest affinity between *Prionogonus* and these two genera, the most southerly in the tribe Apheloriini, but the similarity deserves mention. Both *Cheiropus* and *Stelgipus* are monotypic, and neither has been subjected to a comprehensive treatment. Likewise, the original descriptions of both genera and their single species (Loomis 1944) are inadequate by modern standards and must be redone. An analysis of *Cheiropus* and *Stelgipus* might reveal whether there is a connection between them and *Prionogonus,* or whether this similarity is merely coincidental.

Specific.—The common properties of the sharp anterior bend, the expanded distal extremity of the peak, the presence of a lateral flange, and the location of the solenomerite beneath the peak all point to a close relationship between *haerens* and *divaricatus*. They appear to be only one step removed from a common ancestor (Fig. 15); *thrinax* is more divergent.

Acknowledgments

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